VARIABLES AGGREGATION IN TIME VARYING DISCRETE SYSTEMS

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ABSTRACT

In this work we extend approximate aggregation methods in time discrete linear models to the case of time varying environments. Approximate aggregation consists in describing some features of the dynamics of a general system involving many coupled variables in terms of the dynamics of a reduced system with a few number of variables. We present a time discrete time varying model in which we distinguish two time scales. By using perturbation methods we transform the system to make the global variables appear and build up the aggregated system. The asymptotic relationships between the general and aggregated systems are explored in the cases of a cyclically varying environment and a changing environment in process of stabilization. We show that under quite general conditions the knowledge of the behavior of the aggregated system characterizes that of the general system. The general method is also applied to aggregate a multiregional time dependent Leslie model showing that the aggregated model has demographic rates depending on the equilibrium proportions of individuals in the different patches.

KEYWORDS: Approximate aggregation, population dynamics, time scales, strong ergodicity, cyclic environment.

1. INTRODUCTION

As a consequence of the intrinsic complexity of many ecological systems, modeling biological systems implies dealing with models involving a large number of variables. For example, a community is a set of several interacting populations. Populations themselves are not homogeneous but are composed of many individuals of different ages or in different stages. These stages can correspond to size, genotypes, phenotypes, spatial patches, individual activities, etc. Populations are then subdivided into several subpopulations. Therefore, when modeling ecological systems we are faced to a complexity which partly arises as a consequence of the internal structure of populations.

A first approach to modeling is to try to manage this complexity directly by building a mathematical model which describes the biological system in detail. This has the advantage of including the complexity of the system in the model, but it leads to models with a large number of variables, which are difficult to handle mathematically. Mostly one must use computer simulations which involves dealing with restrictions, generally unknown, concerning robustness of solutions with respect to parameters and initial conditions.

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The contrary approach consists in constructing models that involve a small number of variables, which frequently results in ignoring the internal structure of the population. Populations are then considered as entities and described by a single variable, frequently the total population or density. Associated to this simplification is the assumption that the internal structure of populations is not relevant for the system and therefore can be neglected, i.e., the total system can be approximated by a reduced system. However, this assumption is hardly ever justified and simplified models are used with little or no argumentation regarding the approximations and simplifications needed to build the model.

The use of variables aggregation for treating models represents a compromise between these two approaches. We deal with systems that are complex in the sense of having a large number of variables, and make use of the existence of different time scales (i.e., of biological processes which take place with characteristic times very different from each other) to introduce approximations that allow to substitute the global system by a reduced system that resembles at least some of the properties of the original system. We will refer to the fast process as fast dynamics while the slow process will be denoted by slow dynamics. The use of averaging and perturbation methods in a rigorous way allows one to carry out an approximate aggregation of the global system into an reduced aggregated system which is governed by a small number of slowly varying global variables. Here the term "approximate aggregation" is used to distinguish it from "perfect aggregation", which stands for the exact replacement of the original system by a condensed system and that can only be achieved in very special cases (Iwasa *et al.*, 1989). Besides providing a simple version of the original system, aggregation techniques allow to study the interaction terms between the slow and the fast dynamics which have important ecological significance.

Approximate aggregation has been widely studied in the context of time continuous systems with different time scales for both linear and density dependent models (Auger, 1989; Auger *et al.*, 1993; 1994; 1996).

The aim of this work is to perform variables aggregation in a time discrete model in which the conditions of the environment are changing through time. We will therefore deal with a system of difference equations with non constant coefficients.

Time discrete models are widely used in population dynamics and are particularly well adapted for the study of the life cycle of populations (Caswell, 1989). For example, the Leslie model (Leslie, 1945; Logofet, 1993) describes an age structured population at discrete times. When reproduction occurs periodically each year, the Leslie model, characterized by the so called Leslie matrix, provides the density of each one of the age classes at consecutive generations.

However, the Leslie model does not account for the internal structure of populations. Discrete models for the study of general class structured populations, which are the scope of variable aggregation techniques, can be constructed in a manner analogous to the Leslie models, but they result in projection matrices that, in the general case, are square non-negative matrices (Leftkovitch matrices) (Leftkovitch, 1965).

Aggregation in discrete models has the difficulty of including in the model the two time scales which, unlike the time continuous case, it is not straightforward, which forces to model the fast and the slow dynamics by two different matrices. Previous contributions in the linear case are those of Sánchez *et al.* (1995) and Bravo *et al.* (1995) in which two time discrete models are proposed and aggregated for the time invariant case. In the first model the projection interval coincides with the characteristic time associated to the fast dynamics, whereas in the second the projection interval is that of the slow dynamics. In both cases it was proved that under certain conditions the dominant eigenelements of the general system and of the aggregated system coincide to a certain order. These two models have also been extended to deal with the density dependent case (Bravo *et al.* 1997; in press).

In this work we extend the second model in the linear case to account for the case of a time varying environment. In particular, we will deal with the cases of cyclically varying environment and of an environment in process of stabilization.

The basic ideas behind our approach to approximately aggregate the original system are: 1) to approximate (bounding the error we commit) the original system by another one (auxiliary system) in which the fast dynamics has reached an equilibrium (in the case this equilibrium exists) and 2) to collapse this auxiliary system into a reduced system in such a way that some of the characteristics of the former (in particular asymptotic behavior) can be exactly inferred from those of the latter.

Periodic environment models are relevant because of the pronounced seasonal periodicities in many environments. If environmental differences between years are negligible in comparison with difference between seasons, projection models with a time step shorter than the annual cycle naturally appear to vary in a periodic fashion (MacArthur, 1968). The literature offers different approaches to the study of these models. The classical one (Skellam, 1967), which is the one we will follow, is based in transforming the original system into a time invariant one considering the length of a cycle as the projection interval.

The case of environmental variation tending to stabilization has not been addressed with profusion in the literature, but it responds to important biological considerations. Indeed, environments do not constantly maintain its characteristics, but are frequently subjected to perturbations caused by different incidental climatological conditions such as prolonged droughts or rains, extreme temperatures, etc., which induce perturbations in the vital rates of the population. If we suppose that these perturbations do not alter the equilibrium characteristics of the environment and that the environment progressively regains equilibrium, we might wonder whether, in the long run, the system is independent of those incidental perturbations and depends only of the equilibrium vital rates. Because of the resemblance with the time invariant case, we could also think that under certain conditions the system is strongly ergodic, i.e., it has a fixed asymptotic population structure independent of initial conditions (Cohen, 1979), and its growth is asymptotically exponential. Moreover, we would like to know when that population structure and asymptotic exponential growth are those corresponding to the case when the environment constantly has the equilibrium characteristics. Most of the mathematical results behind this subject are proposed by Seneta (1981).

Section 2 proposes a linear time discrete model which distinguishes time scales in the general case of varying environment and gives a criterium to build the aggregated system. The fast dynamics is supposed to be, for all times, an internal and conservative process for each of the groups (as it is the case for migration, activity changes, etc.) and to have an asymptotic equilibrium distribution among the corresponding subgroups. The aggregated system is shown to have a structure that can easily be related to that of the slow dynamics. In fact, the entries of the matrix that represents the aggregated system are obtained as a linear combination of those that correspond to the slow dynamics, being the coefficients of the combination functions of the equilibrium distribution of the fast dynamics. This general case is also particularized to the case of a multiregional Leslie model (age and patch structured population) in which migration can be considered a fast process in comparison with demography. In this case the demography for the microsystem is given by a block Leslie matrix. Upon aggregating we have that the matrix that represents the aggregated system is a classical Leslie matrix.

Section 3 presents an introduction to the general treatment for cyclical linear systems and establishes as well the relationships between the microsystem and the aggregated system when the environment varies in a cyclical fashion. We show that under wide conditions, if the separation between the time scales of the slow and fast dynamics is sufficiently high, the asymptotic population structure of both systems is cyclical. Besides, both the asymptotic population structure and growth rate for the above mentioned systems can be related in a approximate way (being the approximation perfectly quantified and depending on the separation between the two time scales).The results are also particularized to the formerly mentioned case of an age and patch structured population.

Section 4 has the same structure as section 3, but in this occasion we address the case of an stabilizing environment. In the first place we give sufficient conditions for a general system to exhibit strong ergodicity (tendency towards a fixed population structure independent of the initial conditions) and an exponential asymptotic growth. We also show that under certain assumptions, a sufficient separation of the fast and slow time scales guarantees that both systems are strongly ergodic, and their corresponding asymptotic population structure and growth rate can be related in a precise way as a function of that time scales separation.

2. A DISCRETE MODEL WITH DIFFERENT TIME SCALES

The model we propose is a generalization of the linear discrete model considered in Sánchez *et al.* (1995) in which we want to allow the parameters of the model to be time dependent.

The General System

We suppose a stage-structured population in which population is classified into stages or groups attending to any characteristic of the life cycle. Moreover, each of these groups is divided into several subgroups that can correspond to different spatial patches, different individual activities or any other characteristic that could change the life cycle parameters. The model is therefore general in the sense that we do not state in detail the nature of the population or the subpopulations. In order to illustrate the model and the results, we shall particularize our study to the case when the groups correspond to age and the subgroups characterize the spatial location of the individuals.

We consider the population being subdivided in q populations (or groups). Each group is subdivided in subpopulations (subgroups) in such a way that for each $i = 1,2,\ldots,q$, group i has N_i subgroups. Therefore, the total number of subgroups is $N = N_1 + N_2 + \ldots + N_q$.

We will denote by x_n^{ij} the density of subpopulation j of population i at time n, with $i = 1,2,\ldots,q$ and $j = 1,2,\ldots,N_i$. In order to describe the population of group i we will use vector $\overline{\mathbf{x}}_n^i = \left(x_n^{i1}, x_n^{i2}, \cdots, x_n^{iN_i}\right)^T \in R^{N_i}$, $i = 1,2,...,q$, where T denotes transposition. The composition of the total population is then given by vector $X_n = \left(\overline{x}_n^{1^T}, \overline{x}_n^{2^T}, \cdots, \overline{x}_n^{q^T}\right)^T \in R^N$.

In the evolution of the population we will consider two processes whose corresponding characteristic time scales, and consequently their projection intervals, are very different from each other. In order to include in our model both time scales we will model these two processes, to which we shall refer as the fast and the slow dynamics, by two different matrices.

We shall choose as the projection interval of our model, that corresponding to the slow dynamics, i.e., the time Δt elapsed between times n and $n+1$ is the projection interval of the slow dynamics. In Bravo *et al.* it is proposed and analyzed a model in which its projection interval coincides with that of the fast dynamics.

In principle, we will make no special assumptions regarding the characteristics of the slow dynamics. Thus, for a certain fixed projection interval the slow dynamics will be represented at time n by a non-negative projection matrix $\mathbf{M}_n \in R^{N \times N}$, which in this context is usually referred to as Leftkovitch matrix and which we consider divided into blocks $\mathbf{M}_{ij}(n)$, $1 \le i,j \le q$. We have then

$$\mathbf{M}_n = \begin{bmatrix} \mathbf{M}_{11}(n) & \mathbf{M}_{12}(n) & \cdots & \mathbf{M}_{1q}(n) \\ \mathbf{M}_{21}(n) & \mathbf{M}_{22}(n) & \cdots & \mathbf{M}_{2q}(n) \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{M}_{q1}(n) & \mathbf{M}_{q2}(n) & \cdots & \mathbf{M}_{qq}(n) \end{bmatrix}$$

where each block $\mathbf{M}_{ij}(n)$ has dimensions $N_i \times N_j$ and characterizes the rates of transference of individuals from the subgroups of group j to the subgroups of group i at time n. More specifically, for each $m = 1,2,...,N_i$ and each $l = 1,2,...,N_j$, the entry of row m and column l of $\mathbf{M}_{ij}(n)$ represents the rate of transference, at time n, of individuals from subgroup l of group j to subgroup m of group i.

As far as the fast dynamics is concerned, we suppose that it is for each group $i = 1,2,...,q$, internal, conservative for the total number of individuals and with an asymptotically stable distribution among the subgroups. Besides, we will suppose that the characteristics of the fast dynamics can be considered constant over each of the time intervals $[n, n+1)$.

Therefore, if we consider a fixed projection interval (which will be small in comparison with that chosen for the slow dynamics), the fast dynamics of group i will be represented, during the time interval $[n, n+1)$, by a regular stochastic matrix (i.e., a primitive stochastic matrix) $\mathbf{P}_i(n)$ of dimensions $N_i \times N_i$. The matrix $\mathbf{P}_n$ which represents the fast dynamics for the whole population during that interval is then

$$\mathbf{P}_n = diag(\mathbf{P}_1(n), \mathbf{P}_2(n), ..., \mathbf{P}_q(n)). \tag{2}$$

Since matrices $\mathbf{P}_i(n)$ are regular stochastic, they all verify that their spectral radius is 1 and that they have positive Perron right and left eigenvectors given by $\mathbf{v}_i(n)$ and $\mathbf{e}_i$ respectively, where $\mathbf{e}_i = (1,1,...,1)^T$ has dimensions $N_i \times 1$. We then have

$$\mathbf{P}_i(n)\mathbf{v}_i(n) = \mathbf{v}_i(n) \ ; \ \mathbf{e}_i^T \mathbf{P}_i(n) = \mathbf{e}_i^T \tag{3}$$

Besides, we normalize $\mathbf{v}_i(n)$ so it is a probability vector, that is, $\langle \mathbf{v}_i(n), \mathbf{e}_i \rangle = 1$.

Therefore, if group i were governed constantly and exclusively by the fast dynamics given by matrix $\mathbf{P}_i(n)$, it would have an asymptotically stable distribution given by the positive probability vector $\mathbf{v}_i(n)$.

The Perron-Frobenius theorem assures that the matrix that characterizes the asymptotic behavior of the fast dynamics of group i at time n is

$$\overline{\mathbf{P}}_i(n) = \lim_{k\to\infty} \mathbf{P}_i^k(n) = \left(\mathbf{v}_i(n) \mid \cdots \mid \mathbf{v}_i(n)\right) = \mathbf{v}_i(n)\mathbf{e}_i^T$$

and, therefore, the asymptotic behavior of the fast dynamics for the whole population is given at time n by matrix $\overline{\mathbf{P}}_n = diag\left(\overline{\mathbf{P}}_1(n), \overline{\mathbf{P}}_2(n), \cdots, \overline{\mathbf{P}}_q(n)\right)$.

We define also matrix $\mathbf{V}_n = diag(\mathbf{v}_1(n), \mathbf{v}_2(n), \ldots, \mathbf{v}_q(n))$, that will be used in the subsequent sections and which admits the following interpretation. If we have a non-negative vector of R^q that indicates the total number of individuals included in the different groups and it is multiplied by $\mathbf{V}_n$, we obtain a vector of R^N, which gives how these individuals would be asymptotically distributed among the subgroups, if the system were governed exclusively by the fast dynamics corresponding to the interval $[n, n+1)$.

As we have said before, the projection interval of the model is that corresponding to matrices $\mathbf{M}_n$. We then need to approximate the effect of the fast dynamics over a time interval much longer than its own. In order to do so we will suppose that during each interval $[n, n+1)$ matrix $\mathbf{P}_n$ has operated a number k of times, where k is a big enough integer that can be interpreted as the ratio between the projection intervals corresponding to the slow and fast dynamics. Therefore, the fast dynamics will be modelled by $\mathbf{P}_n^k$ and the proposed model will consist in the following system of N linear difference equations that we denote as "microsystem" or "general system";

$$\mathbf{X}_{n+1} = \mathbf{M}_n \mathbf{P}_n^k \mathbf{X}_n \tag{4}$$

The Aggregated Model

In this section we will approximate the microsystem (4), consisting of N variables (microvariables) associated to the different subgroups, by an aggregated system (or macrosystem) of q variables (global variables), each of them associated to one group.

We define the global variables by

$$y_n^i = x_n^{i1} + x_n^{i2} + \cdots + x_n^{iN_i}; \quad i = 1, 2, \cdots, q$$

which indicate the total number of individuals in each of the groups at the corresponding time.

These global variables, that we represent by vector $\mathbf{Y}_n \in R^q$, can be obtained from vector $\mathbf{X}_n$ by multiplying by matrix $\mathbf{U} = diag\left(\mathbf{e}_1^T, \mathbf{e}_2^T, \cdots, \mathbf{e}_q^T\right)$, that is

$$\mathbf{Y}_n = (y_n^1, \cdots, y_n^q) = \mathbf{U}\mathbf{X}_n \tag{6}$$

The following Lemma states some properties of matrices $\mathbf{P}_n, \overline{\mathbf{P}}_n, \mathbf{V}_n$ and $\mathbf{U}$ that will be frequently used through the paper.

LEMMA 1. *Matrices* $\mathbf{P}_n, \overline{\mathbf{P}}_n, \mathbf{V}_n$ *and* $\mathbf{U}$ *verify, for all n :*

a) $\overline{\mathbf{P}}_n\mathbf{P}_n = \mathbf{P}_n\overline{\mathbf{P}}_n = \overline{\mathbf{P}}_n\overline{\mathbf{P}}_n$

b) $\mathbf{P}_n\mathbf{V}_n = \overline{\mathbf{P}}_n\mathbf{V}_n = \mathbf{V}_n$

c) $\mathbf{U}\overline{\mathbf{P}}_n = \mathbf{U};\ \mathbf{U}\mathbf{V}_n = \mathbf{I}_q;\ \overline{\mathbf{P}}_n = \mathbf{V}_n\mathbf{U}$

If in the general system (4) we multiply by matrix $\mathbf{U}$

$$\mathbf{U}\mathbf{X}_{n+1} = \mathbf{U}\mathbf{M}_n\mathbf{P}_n^k\mathbf{X}_n \tag{7}$$

we get the global variables in the first member, but we do not obtain an autonomous system on these variables.

If system (7) were autonomous on the global variables, it would have been an example of what is called perfect aggregation (Iwasa *et al.,* 1987), which is only possible in very particular cases. In fact, what the possibility of perfect aggregation indicates is that the study of the original system can be simplified with just a better choice for the state variables, and so it is the global variables which best describe the system under consideration.

In order to simplify the general system we then resort to approximate aggregation. For this we consider an auxiliary system (that we will call non-perturbed system), which approximates the behavior of the general system and that is susceptible of being perfectly aggregated. This auxiliary system is the result of considering the microsystem in the case that fast dynamics has reached its asymptotic equilibrium, i.e.,

$$\mathbf{X}_{n+1} = \mathbf{M}_n\overline{\mathbf{P}}_n\mathbf{X}_n \tag{8}$$

This system approximates the microsystem in the following sense; since $\lim_{k\to\infty}\mathbf{P}_n^k = \overline{\mathbf{P}}$ and $\mathbf{M}_n\mathbf{P}_n^k = \mathbf{M}_n\overline{\mathbf{P}}_n + \mathbf{M}_n(\mathbf{P}_n^k - \overline{\mathbf{P}}_n)$ we can consider matrix $\mathbf{M}_n\mathbf{P}_n^k$ as being a perturbation of matrix $\mathbf{M}_n\overline{\mathbf{P}}_n$.

In order to show that (8) can be perfectly aggregated let us multiply both members by matrix $\mathbf{U}$

$$\mathbf{U}\mathbf{X}_{n+1} = \mathbf{U}\mathbf{M}_n\overline{\mathbf{P}}_n\mathbf{X}_n = \mathbf{U}\mathbf{M}_n\mathbf{V}_n\mathbf{U}\mathbf{X}_n$$

and then we obtain the aggregated system

$$\mathbf{Y}_{n+1} = \overline{\mathbf{M}}_n\mathbf{Y}_n \tag{9}$$

where matrix $\overline{\mathbf{M}}_n \in R^{q\times q}$ is given by $\overline{\mathbf{M}}_n = \mathbf{U}\mathbf{M}_n\mathbf{V}_n$, and has the form

$$\overline{\mathbf{M}}_n = \begin{bmatrix} \mathbf{e}_1^T\mathbf{M}_{11}(n)\mathbf{v}_1(n) & \mathbf{e}_1^T\mathbf{M}_{12}(n)\mathbf{v}_2(n) & \cdots & \mathbf{e}_1^T\mathbf{M}_{1q}(n)\mathbf{v}_q(n) \\ \mathbf{e}_2^T\mathbf{M}_{21}(n)\mathbf{v}_1(n) & \mathbf{e}_2^T\mathbf{M}_{22}(n)\mathbf{v}_2(n) & \cdots & \mathbf{e}_2^T\mathbf{M}_{2q}(n)\mathbf{v}_q(n) \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{e}_q^T\mathbf{M}_{q1}(n)\mathbf{v}_1(n) & \mathbf{e}_q^T\mathbf{M}_{q2}(n)\mathbf{v}_2(n) & \cdots & \mathbf{e}_q^T\mathbf{M}_{qq}(n)\mathbf{v}_q(n) \end{bmatrix} \tag{10}$$

Therefore we have that for each time n the element of row i and column j of the matrix of the aggregated model is $\mathbf{e}_i^T\mathbf{M}_{ij}(n)\mathbf{v}_j(n) = \Sigma_{m,l}M_{ij}^{ml}(n)v_j^l(n)$ which is a weighted linear combination of the coefficients of the slow dynamics at time n corresponding to the transference from group j to group i. Notice that the weights are given by the equilibrium distribution of the fast dynamics at time n. ($M_{ij}^{ml}(n)$ denotes the element of row m and column l of $\mathbf{M}_{ij}(n)$ and $v_j^l(n)$ the l-th component of $\mathbf{v}_j(n)$).

The following sections will be devoted to the study of the relationships between the different systems defined above in the hypothesis of cyclically varying environment and stabilizing environment.

The following lemma, which is a trivial consequence of (10) and of the fact of vectors $\mathbf{v}_i(n)$ and $\mathbf{e}_i$ being positive for all i and n, allows us to relate the structure of matrices $\mathbf{M}_n$ and $\overline{\mathbf{M}}_n$.

LEMMA 2. *For all n,* $\overline{\mathbf{M}}_n$ *is a nonnegative matrix in which the element of row i and column j of* $\overline{\mathbf{M}}_n$ *is non-zero if and only if matrix* $\mathbf{M}_{ij}(n)$ *is not zero.*

Notice from this last result that the pattern of non-zero elements in $\overline{\mathbf{M}}_n$ coincides with the pattern of non-zero blocks $\mathbf{M}_{ij}(n)$ for the slow dynamics.

An Age-patch Structured Model with Fast Migration

In order to illustrate how the proposed model and the aggregation procedure would work in a special case for the fast and slow processes, we will consider an multiregional Leslie model, i.e., an age-structured population where we distinguish several different spatial patches in every age class. Therefore, two biological processes govern the evolution of our model, demography and migration. These kind of models have been frequently treated in the literature (Caswell, 1989; Logofet, 1993) although not with the approach of distinguishing different time scales in those two processes. On the contrary we shall show that, as is usually the case in nature, migration can be considered a fast process with respect to demography.

We suppose that there are q age classes and that for each age class i individuals are spread out in N_i spatial patches among which they may migrate.

Keeping the notation of the preceding section we denote by x_n^{ij} the number of individuals of age i in the j-th spatial patch at time n, with $i = 1,2,...,q$ and $j = 1,2,...,N_i$. We suppose also that the migration for individuals of age i is represented at time n by a primitive matrix $\mathbf{P}_i(n)$. Since migration conserves the total number of individuals for each group we have that $\mathbf{P}_i(n)$ will be an stochastic matrix and therefore the fast dynamics meets the requirements of the last section. Each vector $\mathbf{v}_i(n)$ gives the equilibrium distribution corresponding to the migratory process for group i at time n.

Demography will be represented by a generalized Leslie matrix in the following way:

$$\mathbf{M}_n = \begin{bmatrix} \mathbf{M}_{11}(n) & \mathbf{M}_{12}(n) & \cdots & \mathbf{M}_{1q}(n) \\ \mathbf{M}_{21}(n) & \mathbf{M}_{22}(n) & \cdots & \mathbf{M}_{2q}(n) \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{M}_{q1}(n) & \mathbf{M}_{q2}(n) & \cdots & \mathbf{M}_{qq}(n) \end{bmatrix} = \begin{bmatrix} \mathbf{F}_1(n) & \mathbf{F}_2(n) & \cdots & \mathbf{F}_{q-1}(n) & \mathbf{F}_q(n) \\ \mathbf{S}_1(n) & 0 & \cdots & 0 & 0 \\ 0 & \mathbf{S}_2(n) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \mathbf{S}_{q-1}(n) & 0 \end{bmatrix}$$

where $\mathbf{F}_i(n) = [F_{kl}^i(n)] \in R^{N_1 \times N_i}$, $i = 1,...,q$; $\mathbf{S}_i(n) = [S_{kl}^i(n)] \in R^{N_{i+1} \times N_i}$, $i = 1,...,q-1$ and where the coefficients are divided into two classes as in the classical Leslie model.

Fertility coefficients; $F_{kl}^{i}(n)$ = transference coefficient from spatial patch l and age i to spatial patch k and age 1 during interval $[n, n + 1)$. $k = 1,\ldots,N^1$; $l = 1,\ldots,N^i$; $i = 1,\ldots,q$.

Aging coefficients: $S_{kl}^{i}(n)$ = transference coefficient from spatial patch l and age i to spatial patch k and age $i + 1$ during interval $[n, n+1)$. $k = 1,\ldots,N^{i+1}$; $l = 1,\ldots,N^i$; $i = 1,\ldots,q-1$. These coefficients must verify the consistency condition $\sum_{k=1}^{N^{i+1}} S_{kl}^{i}(n) \leq 1$.

According to (13), the aggregated system will have the form of a classical Leslie matrix:

$$\overline{\mathbf{M}}_n = \begin{bmatrix} f_1(n) & f_2(n) & \cdots & f_{q-1}(n) & f_q(n) \\ s_1(n) & 0 & \cdots & 0 & 0 \\ 0 & s_2(n) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{q-1}(n) & 0 \end{bmatrix}$$

where we have:

Fertility coefficients at time n : $f_i(n) = \mathbf{e}_1^T \mathbf{F}_i(n)\mathbf{v}_i(n), \quad i = 1, \ldots, q$.

Survival coefficients at time n : $s_i(n) = \mathbf{e}_{i+1}^T \mathbf{S}_i(n)\mathbf{v}_i(n), \quad i = 1, \ldots, q-1$.

Notice that a) $f_i(n)$ is a weighted linear combination of the fertility coefficients of group i at time n being the weights the coefficients of the equilibrium spatial distribution among the different patches for the migration of group i. Something analogous holds for $s_i(n)$. b) lemma 2 assures that $f_i(n)$ is different from zero if and only if matrix $\mathbf{F}_i$(n) is. In the same way, $s_i(n)$ is different from zero if and only if matrix $\mathbf{S}_i$(n) is. We see, then, that matrix $\overline{\mathbf{M}}_n$ retains the structure of the non-zero blocks $\mathbf{M}_{ij}(n)$ of $\mathbf{M}_n$.

3. CYCLICALLY VARYING ENVIRONMENT

In this section we shall develop results that allow one to approximate the asymptotic behavior of the general system given that of the aggregated system in the case of a cyclically varying environment, that is, in the case where we have matrices $\mathbf{M}_n$ and $\mathbf{P}_n$ verifying $\mathbf{P}_{n+\tau} = \mathbf{P}_n$ and $\mathbf{M}_n = \mathbf{M}_{n+\tau}$ for all n where τ is the period of the cyclical variation.

The General Approach

The literature offers several techniques for the study of discrete models

$$\mathbf{z}_{n+1} = \mathbf{A}_n \mathbf{z}_n \tag{11}$$

with cyclical variability. The classical approach (Skellam, 1967; Caswell, 1989), which is the one we shall use in our subsequent development, is to study the system at times separated by τ units considering products of matrices of length τ. Other approaches to the study of discrete systems with cyclical variability are those of Tuljapurkar (1985) and Gourley and Lawrence (1977), that although have some advantages regarding information extraction from the life cycle, are not well suited for our aggregation techniques.

Following Skellam, for each $s \in \{0,1,...,\tau-1\}$ and all $m = 1,2,...$ we have from system (11)

$$\mathbf{z}_{s+(m+1)\tau} = \mathbf{A}_{s+\tau-1} \cdots \mathbf{A}_{s+1}\mathbf{A}_s\mathbf{z}_{s+m\tau} \quad (12)$$

and, if we define $\mathbf{B}_s = \mathbf{A}_{s+\tau-1} \ldots \mathbf{A}_{s+1} \mathbf{A}_s$, is

$$\mathbf{z}_{s+(m+1)\tau} = \mathbf{B}_s\mathbf{z}_{s+m\tau} \quad (13)$$

so we can study the population at times s, $s+\tau$, $s+2\tau$... considering matrix $\mathbf{B}_s$, which is independent of m, making use of the time invariant theory. Therefore, if we assume $\mathbf{B}_s$ has an strictly dominant eigenvalue μ_s, then μ_s gives the asymptotic growth rate per τ time steps of the population (and so $(\mu_s)^{\frac{1}{\tau}}$ is the asymptotic growth rate per time step). For this analysis to be consistent, it must be μ_s (and the rest of the eigenvalues of $\mathbf{B}_s$) independent of the observation points, that is, $\mu_0 = \cdots = \mu_{\tau-1} = \mu$ independent of s. This is of course the case, since $\mathbf{B}_0$, $\mathbf{B}_1$,...,$\mathbf{B}_{s-1}$ are products of the same factors in cyclical permutation and therefore all have the same characteristic polynomial (Horn & Johnson, 1985, page 53). Concerning the stable population vectors, it is trivial to show that if $\mathbf{w}_s$ is a probability normed eigenvector of $\mathbf{B}_s$ associated to μ (and therefore the structure of the population at times $s + m\tau$ is asymptotically given by $\mathbf{w}_s$) then for any s' (lets say $s' > s$) $w_{s'} = \mathbf{A}_{s'-1} \cdots \mathbf{A}_{s+1}\mathbf{A}_s\mathbf{w}_s$ is eigenvector of $\mathbf{B}_{s'}$ (not necessarily normalized) associated to μ and, consequently, the population at times $s' + m\tau$ asymptotically has the direction of $\mathbf{w}_{s'}$. Notice that it is $\mathbf{w}_{s+\tau} = \mu\mathbf{w}_s$, so we have that the population structure is asymptotically cyclic with a period not greater than τ.

It is important to take into account that even though $\mathbf{B}_0$, $\mathbf{B}_1$,..., $\mathbf{B}_{s-1}$ have the same eigenvalues including multiplicities, the irreducibility or the primitivity of one of the $\mathbf{B}_s$ does not imply the irreducibility or primitivity of the rest.

As a result of the above discussions we can study system (12) without loss of generality by just choosing $s \in \{0,1,...,\tau-1\}$ (for example $s = 0$) and then dealing with system (13).

Asymptotic Relationships for the Macro and Micro Models

We will now apply the above technique to treat the aggregated, auxiliary and original systems constructed in the last section for the case of a cyclically varying environment. We have then as an starting assumption:

H1. Matrices $\mathbf{M}_n$ and $\mathbf{P}_n$ are periodic with period τ.

In the first place we will set out the equations that govern these systems taking as time step that corresponding to a cycle.

Let us consider $s = 0$ (for any other s the treatment would be absolutely analogous). The microsystem (4) can be put in the form:

$$\mathbf{X}_{(m+1)\tau} = \mathbf{C}(k)\mathbf{X}_{m\tau} \quad (14)$$

where $\mathbf{C}(k)$ is given by

$$\mathbf{C}(k) = \mathbf{M}_{\tau-1}\mathbf{P}_{\tau-1}^k \ldots \mathbf{M}_1\mathbf{P}_1^k\mathbf{M}_0\mathbf{P}_0^k. \quad (15)$$

In a similar way we have for the auxiliary system (8)

$$\mathbf{X}_{(m+1)\tau} = \mathbf{C}'\mathbf{X}_{m\tau} \tag{16}$$

with

$$\mathbf{C}' = \mathbf{M}_{\tau-1}\overline{\mathbf{P}}_{\tau-1}\ldots\mathbf{M}_1\overline{\mathbf{P}}_1\mathbf{M}_0\overline{\mathbf{P}}_0 \tag{17}$$

In order to shorten the notation we will define

$$\mathbf{B} = \mathbf{M}_{\tau-1}\overline{\mathbf{P}}_{\tau-1}\ldots\mathbf{M}_1\overline{\mathbf{P}}_1\mathbf{M}_0$$

so we have $\mathbf{C}' = \mathbf{B}\overline{\mathbf{P}}_0$.

Finally, the aggregated system (9) referred to a cycle has the form

$$\mathbf{Y}_{(m+1)\tau} = \overline{\mathbf{C}}\,\mathbf{Y}_{m\tau} \tag{18}$$

where the global variables are those defined in (6) and matrix $\overline{\mathbf{C}} \in R^{q\times q}$ is given by

$$\overline{\mathbf{C}} = \overline{\mathbf{M}}_{\tau-1}\overline{\mathbf{M}}_1\overline{\mathbf{M}}_0 = \mathbf{U}\mathbf{M}_{\tau-1}\mathbf{V}_{\tau-1}\ldots\mathbf{U}\mathbf{M}_0\mathbf{V}_0 = \mathbf{U}\mathbf{C}'\mathbf{V}_0\mathbf{U}\mathbf{B}\mathbf{V}_0$$

where we have used lemma 1 in the last two equalities.

The purpose for this construction is to characterize the asymptotic behavior of the general system at times multiple of τ (i.e., at times of the form $m\tau$ with m asymptotically large) supposed the asymptotic behavior of the aggregated system is known. We will proceed as follows. In the first place we will relate the spectral properties of matrices $\mathbf{C}'$ and $\overline{\mathbf{C}}$, which will yield the relationship between the asymptotic behavior of the auxiliary and aggregated system. Later, by considering $\mathbf{C}(k)$ as a perturbation of $\mathbf{C}'$, we will compare the asymptotic elements of both matrices, which will relate the behavior of the auxiliary and original systems.

The following proposition relates the spectral properties of matrices $\mathbf{C}'$ and $\overline{\mathbf{C}}$.

PROPOSITION 1. *Matrices* $\mathbf{C}'$ *and* $\overline{\mathbf{C}}$ *verify:*

a) $\det(\lambda\mathbf{I}_N - \mathbf{C}') = \lambda^{N-q}\det(\lambda\mathbf{I}_q - \overline{\mathbf{C}})$; *in particular, the dominant eigenvalues of both matrices, together with their respective multiplicities, coincide.*

b) If $\mathbf{r}$ *and* $\mathbf{l}$ *are, respectively, right and left eigenvectors of* $\overline{\mathbf{C}}$ *associated to* $\lambda \neq 0$ *then* $\mathbf{B}\mathbf{V}_0\mathbf{r}$ *and* $\mathbf{U}^T\mathbf{l}$ *are respectively right and left eigenvectors of* $\mathbf{C}'$ associated to λ.

Proof. See appendix.

For our study we make the following assumption:

H2. $\overline{\mathbf{C}}$ has a simple and strictly dominant eigenvalue μ (necessarily positive), with associated right and left eigenvectors $\mathbf{r}$ and $\mathbf{l}$, respectively.

Recall that the incidence matrix of a non-negative matrix $\mathbf{A}$ is a matrix $G(\mathbf{A})$ of the same dimensions as $\mathbf{A}$ given by $G(\mathbf{A})_{ij} = 1$ if $A_{ij} > 0$ and $G(\mathbf{A})_{ij} = 0$ if $A_{ij} = 0$. Two non-negative matrices $\mathbf{A}$ and $\mathbf{B}$ of the same dimensions are then said to have the same incidence matrix (and we will denote it $\mathbf{A} \sim \mathbf{B}$) when both matrices have their non-zero elements in corresponding positions. The properties of irreducibility, reducibility, primitivity, etc., of a non-negative matrix $\mathbf{A}$ are functions only of the incidence matrix of $\mathbf{A}$ and not of the actual values of its non-zero elements.

Of course, a sufficient condition for $\overline{\mathbf{C}}$ to meet H2 is that $\overline{\mathbf{C}}$ is primitive. In the frequent case that all $\mathbf{M}_n$ and all $\mathbf{P}_n$ have the same incidence matrix (i.e., $\mathbf{M}_n \sim \mathbf{M}_{n'}$ and $\mathbf{P}_n \sim \mathbf{P}_{n'}$ for all n and n'), a necessary and sufficient condition for $\overline{\mathbf{C}}$ to be primitive is that any of the $\overline{\mathbf{M}}_n$ (and therefore all of them) is primitive. From proposition 2 we have that $\overline{\mathbf{M}}_n$ is primitive if and only if $\mathbf{M}_n$ is "block primitive", i.e., the non-zero blocks $\mathbf{M}_{ij}(n)$ are distributed in a primitive pattern. In the case that the $\overline{\mathbf{M}}_n$ are Leslie matrices with not necessarily the same incidence matrices, Keller (1980) and Taylor (1985) give sufficient conditions for the irreducibility and the primitivity of the product in terms of the incidence matrices of each of the factors.

Then, if the aggregated system (9) has a non-negative initial condition $\mathbf{Y}_0$, its asymptotic behavior at times multiple of τ will be given by

$$\lim_{m\to\infty}\frac{\mathbf{Y}_{m\tau}}{\mu^m}=\lim_{m\to\infty}\left(\frac{\overline{\mathbf{C}}}{\mu}\right)^m\mathbf{Y}_0=\frac{\langle \mathbf{l},\mathbf{Y}_0\rangle}{\langle \mathbf{l},\mathbf{r}\rangle}\mathbf{r}$$

Using proposition 1 , we have for the auxiliary system (8):

PROPOSITION 2. *If H1 and H2 hold, then for any non-negative initial condition* $\mathbf{X}_0$ *system (8) verifies:*

$$\lim_{m\to\infty}\frac{\mathbf{X}_{m\tau}}{\mu^m}=\lim_{m\to\infty}\left(\frac{\mathbf{C}'}{\mu}\right)^m\mathbf{X}_0=\frac{\langle \mathbf{l},\mathbf{U}\mathbf{X}_0\rangle}{\langle \mathbf{l},\mathbf{r}\rangle}\frac{1}{\mu}\mathbf{B}\mathbf{V}_0\mathbf{r}$$

Proof. Since μ is simple and strictly dominant eigenvalue for $\overline{\mathbf{C}}$ with associated right and left eigenvectors $\mathbf{r}$ and $\mathbf{l}$ we have from proposition 1, that μ will be simple and strictly dominant eigenvalue for $\mathbf{C}'$ and $\mathbf{B}\,\mathbf{V}_0\mathbf{r}$ and $\mathbf{U}^T\mathbf{l}$ associated right and left eigenvectors. Then

$$\begin{aligned}\lim_{m\to\infty}\frac{\mathbf{X}_{m\tau}}{\mu^m}&=\lim_{m\to\infty}\left(\frac{\mathbf{C}'}{\mu}\right)^m\mathbf{X}_0=\frac{\langle \mathbf{U}^T\mathbf{l},\mathbf{X}_0\rangle}{\langle \mathbf{U}^T\mathbf{l},\mathbf{B}\mathbf{V}_0\mathbf{r}\rangle}\mathbf{B}\mathbf{V}_0\mathbf{r}=\\&=\frac{\langle \mathbf{l},\mathbf{U}\mathbf{X}_0\rangle}{\langle \mathbf{l},\mathbf{U}\mathbf{B}\mathbf{V}_0\mathbf{r}\rangle}\mathbf{B}\mathbf{V}_0\mathbf{r}=\frac{\langle \mathbf{l},\mathbf{U}\mathbf{X}_0\rangle}{\langle \mathbf{l},\mu\mathbf{r}\rangle}\mathbf{B}\mathbf{V}_0\mathbf{r}=\frac{\langle \mathbf{l},\mathbf{U}\mathbf{X}_0\rangle}{\langle \mathbf{l},\mathbf{r}\rangle}\frac{1}{\mu}\mathbf{B}\mathbf{V}_0\mathbf{r}\end{aligned}$$

as we wanted to prove.

Let us now study the asymptotic behavior of the microsystem (4). For $n=0,1,\ldots,\tau-1$ let us consider the eigenvalues of $\mathbf{P}_n$ ordered by decreasing modulus (notice that the eigenvalues of $\mathbf{P}_n$ are the union of those of the different $\mathbf{P}_i(n)$)

$$1=\lambda_1(n)=\ldots=\lambda_q(n)>|\lambda_{q+1}(n)|\geq\ldots\geq|\lambda_N(n)|$$

and let

$$\alpha>\max\{|\lambda_{q+1}(0)|,|\lambda_{q+1}(1)|,\ldots,|\lambda_{q+1}(\tau-1)|\} \tag{20}$$

, i.e., α is any real number greater than the modulus of the "subdominant" eigenvalues of $\mathbf{P}_0,\ldots,\mathbf{P}_{\tau-1}$. Then we have:

PROPOSITION 3. *If* $\|*\|$ *is any consistent matrix norm in the space of real matrices* $N\times N$ *then*

$$\|\mathbf{C}(k)-\mathbf{C}'\|=o(\alpha^k)\quad\text{when}\quad k\to\infty$$

Proof. See appendix.

Notice that since $|\lambda_{q+1}| < 1$, then α can be taken smaller than one and therefore this last result guarantees that $\mathbf{C}(k)$ can indeed be considered a small perturbation of $\mathbf{C}'$ for large k.

We will now relate the dominant spectral elements of matrices $\mathbf{C}(k)$ and $\mathbf{C}'$. In order to do so we make use of the theorem stated in the appendix.

PROPOSITION 4. *For sufficiently high k, matrix* $\mathbf{C}(k)$ *has a simple and strictly dominant eigenvalue* μ_k *that can be expressed in the form*

$$\mu_k = \mu + \frac{\left\langle \mathbf{U}^T \mathbf{l}, \left(\mathbf{C}(k) - \mathbf{C}'\right)\mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle}{\left\langle \mathbf{U}^T \mathbf{l}, \mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle} + o(\alpha^{2k}) = \mu + o(\alpha^k)$$

Besides, associated to μ_k *there are right and left eigenvectors that can be written in the form*

$$\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)$$
$$\mathbf{U}^T\mathbf{l} + o(\alpha^k)$$

Proof. See appendix.

As a consequence of the preceding results, the population vector of the microsystem (4) will have an asymptotic behavior (for times multiple of τ) related to that of the aggregated system by the following proposition.

PROPOSITION 5. *Given H1 and H2 hold, system (4) verifies, for k (big enough) and for any non-negative initial condition* $\mathbf{X}_0$ *:*

$$\lim_{m\to\infty} = \frac{\mathbf{X}_{m\tau}}{(\mu_k)^m} = \lim_{m\to\infty}\left(\frac{\mathbf{C}(k)}{\mu_k}\right)^m \mathbf{X}_0 = \frac{\left\langle \mathbf{l}, \mathbf{U}\mathbf{X}_0\right\rangle}{\left\langle \mathbf{l}, \mathbf{r}\right\rangle}\frac{1}{\mu}\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)$$

where α *is any number verifying (20).*

Proof. From proposition 4 we have

$$\begin{aligned}
\lim_{m\to\infty}\frac{\mathbf{X}_{m\tau}}{(\mu_k)^m} &= \frac{\left\langle \mathbf{U}^T\mathbf{l} + o(\alpha^k), \mathbf{X}_0\right\rangle}{\left\langle \mathbf{U}^T\mathbf{l} + o(\alpha^k), \mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)\right\rangle}\left(\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)\right) \\
&= \frac{\left\langle \mathbf{l}, \mathbf{U}\mathbf{X}_0\right\rangle + o(\alpha^k)}{\left\langle \mathbf{l}, \mathbf{U}\mathbf{B}\mathbf{V}_0\mathbf{r}\right\rangle + o(\alpha^k)}\left(\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)\right) = \\
&= \left(\frac{\left\langle \mathbf{l}, \mathbf{U}\mathbf{X}_0\right\rangle}{\mathbf{l}, \mu\mathbf{r}} + o(\alpha^k)\right)\left(\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)\right) = \frac{\left\langle \mathbf{l}, \mathbf{U}\mathbf{X}_0\right\rangle}{\mathbf{l}, \mathbf{r}}\frac{1}{\mu}\mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)
\end{aligned}$$

For any $s \in \{0,1,\ldots,\tau-1\}$ we therefore have

$$\lim_{m\to\infty}\frac{\mathbf{X}_{m\tau+s}}{(\mu_k)^m} = \mathbf{M}_{s-1}\mathbf{P}_{s-1}^k \ldots \mathbf{M}_0\mathbf{P}_0^k \lim_{m\to\infty}\frac{\mathbf{X}_{m\tau}}{(\mu_k)^m} =$$
$$= \frac{\langle \mathbf{l}, \mathbf{U}\mathbf{X}_0\rangle}{\langle \mathbf{l}, \mathbf{r}\rangle}\frac{1}{\mu}\mathbf{M}_{s-1}\mathbf{P}_{s-1}^k \ldots \mathbf{M}_0\mathbf{P}_0^k \mathbf{B}\mathbf{V}_0\mathbf{r} + o(\alpha^k)$$

Notice that the asymptotic behavior of the microsystem can be inferred from that of the aggregated system.

Cyclically Varying Demography and Migration

In order to illustrate the above results, we shall study the system proposed in section 2.3.(slow demography and fast migration) in the case that both demography and migration are periodic functions of time, being τ the period. For all n and all $i = 1,\ldots,q$ is then $\mathbf{P}_i(n+\tau) = \mathbf{P}_i(n)$; $F_{kl}^i(n+\tau) = F_{kl}^i(n)$, $k = 1,\ldots, N^1$ $l = 1,\ldots, N^i$ and $S_{kl}^i(n+\tau) = S_{kl}^i(n)$, $k = 1,\ldots,N^{i+1}$; $l = 1,\ldots, N^i$.

For simplicity we make the following assumptions that, as it is immediate to check, will be sufficient conditions for H2 to hold:

1) The incidence matrix for the demography is constant through time, i.e., $\mathbf{M}_n \sim \mathbf{M}_{n'}$ for all n and n'. Therefore, if a vital rate is non-zero initially it remains non-zero subsequently.

2) There is at least a non-zero coefficient in the last age class, that is, $\mathbf{F}_q(n) \neq 0$ for all n and, besides, there exists j such that $m.c.d.(j,q)=1$ and there is at least a non-zero fertility coefficient in age class j (i.e., $\mathbf{F}_j(n) \neq 0$ for all n).

3) For all the age classes there is at least a non-zero survival coefficient, i.e., $\mathbf{S}_i(n) \neq 0$ for all $i = 1,\ldots, q-1$ and all n.

Thus, the results developed in this section are valid for our age and patch structured model. Therefore, the aggregated model will have an asymptotic cyclical behavior with period τ. Let us suppose that the asymptotic growth rate for a cycle in the aggregated model is μ and that the population structure at times $m\tau$ (with m large) is given by the direction of vector $\mathbf{r}$. Then, our results show that the original model will also have an asymptotic cyclical behavior with period τ and that the asymptotic growth rate (for a cycle) and population structure for this system will be $\lambda + o(\alpha^k)$ and $\mathbf{BV}_0\mathbf{r}+o(\alpha^k)$ respectively. In this way, we can approximate the asymptotic behavior of the microsystem given that of the aggregated system is known. The higher k is, i.e., the higher the ratio between the characteristic times of demography and migration is, the more accurate the approximation will be.

4. STABILIZING ENVIRONMENT

This section deals with the treatment of the systems (4), (8) and (9) in the case in which the environment has a temporal variation that tends to stabilization.

We have then as a starting assumption that $\mathbf{M}_n$ and $\mathbf{P}_n$ evolve in the way that there exist matrices $\mathbf{M}$ and $\mathbf{P}$ such that

$$\lim_{n\to\infty}\mathbf{M}_n = \mathbf{M}\,;\ \lim_{n\to\infty}\mathbf{P}_n = \mathbf{P}$$

Obviously, matrices $\mathbf{M}$ and $\mathbf{P}$ would represent the slow and the fast dynamics for the general system in the stabilized environment, that is, for asymptotically large time.

The General Approach

In the first place, we shall address ourselves to the problem with a general system of the kind

$$z_{n+1} = \mathbf{A}_n \mathbf{z}_n \qquad (21)$$

where $\mathbf{z}_n \in R^N$ and $\mathbf{A}_n$ is a sequence of non-negative (not necessarily converging) $N \times$ N matrices. If $\mathbf{z}_p \neq 0$ is the population vector at time $p \geq 0$, we obviously have for all $n \geq p$, $\mathbf{z}_n = \mathbf{A}_{n-1} \ldots \mathbf{A}_{p+1} \mathbf{A}_p \mathbf{z}_p$ and, therefore, in order to study the asymptotic behavior of (21) we have to deal with infinite backwards products of non-negative matrices.

Let us denote by $\|*\|$ the 1-norm in R^N ,that is, if $\mathbf{z} = (z_1 , z_2 ,..., z_N)^T$ is $\|z\| = |z_1| + |z_2| + \ldots + |z_N|$. Then, the total population of system (21) at time n is $\|\mathbf{z}_n\|$ and the population structure at time n will be given by $\frac{\mathbf{z}_n}{\|\mathbf{z}_n\|}$.

Let us define a measure of asymptotic growth rate for system (21). In the time invariant case with constant matrix $\mathbf{A}$ (where we suppose that $\mathbf{A}$ is primitive) we use as measure of growth rate the dominant eigenvalue λ of $\mathbf{A}$, since we have that for any non-zero initial condition $\mathbf{z}_0$ is $\lim_{n\to\infty} \frac{\|\mathbf{z}_{n+1}\|}{\|\mathbf{z}_n\|} = \lim_{n\to\infty} \|\mathbf{z}_n\|^{\frac{1}{n}} = \lambda$. Similarly, in the time varying case we might wonder whether there exists a positive number μ such that for all $\mathbf{z}_0 \neq 0$ is $\lim_{n\to\infty} \|\mathbf{z}_n\|^{\frac{1}{n}} = \mu$ and then define the asymptotic growth rate as μ. It is clear that in the general case (when there are no additional restrictions upon the sequence $\mathbf{A}_n$) neither the population structure of (21) will converge nor there will be any μ verifying the condition above.

Let us consider now the case when the sequence $\mathbf{A}_n$ converges to a (necessarily non-negative) matrix $\mathbf{A}$. Intuitively, we could think that, since for sufficiently large time matrices $\mathbf{A}_n$ are as close to $\mathbf{A}$ as desired, the asymptotic behavior of the system might only depend on the characteristics of matrix $\mathbf{A}$, being therefore independent of 1) the actual sequence $\mathbf{A}_n$ and 2) the time p where we consider the population starting to evolve. Moreover, we could think that (21) might asymptotically behave as the following system

$$\mathbf{z}_{n+1} = \mathbf{A}\mathbf{z}_n \qquad (22)$$

i.e., (21) would asymptotically behave as if the environment were constant and equal to the equilibrium environment and so we could ignore the deviations from this equilibrium. In that case, if we suppose that $\mathbf{A}$ is primitive with dominant eigenvalue λ and probability normed associated eigenvector $\mathbf{v}$, system (21) would have, for any non-zero population vector at time p, an asymptotic growth rate and population structure given by λ and $\mathbf{v}$ respectively.

Notice that besides convergence, some restrictions on $\mathbf{A}_n$ are easily seen to be necessary for the above results to hold. Indeed, if sequence $\mathbf{A}_n$ were such that at some time n_0 the population vector became zero, it would remain to be zero for all subsequent times, not being therefore independent of the sequence $\mathbf{A}_n$.

As a matter of fact, we shall show that if sequence $\mathbf{A}_n$ is such that, a) independently of the initial time p and the initial condition z_p, the population vector can never become zero and b) matrix $\mathbf{A}$ is primitive, then all of the above conjectures are true.

The property by which the structure of solutions of (21) tend to approach a constant vector independently of the initial time and the (non-zero) initial condition, is referred to as strong ergodicity. In the case of deterministic environments, this concept has almost exclusively been used to designate the tendency towards a fixed population structure for a constant environment, what follows as a corollary of the Perron-Frobenius theorem (Cohen, 1979a). Seneta (1981) extended the concept of strong ergodicity to account for the case of non necessarily constant environments, and gave both necessary and sufficient conditions for it to hold.

The study of asymptotic growth rates in variable environments has been addressed to by many authors in the context of stochastic environments (see for example Tuljapurkar *et al.*, 1980; Cohen, 1979b among others). The case of deterministic varying environments has been investigated by Thompson (1978) and Artzrouni (1985) for age structured populations and not necessarily converging vital rates.

Let us introduce some concepts that will be useful to deal with strong ergodicity. A non-negative matrix **A** is said to be column-allowable (row-allowable) if it has at least a non-zero element in each one of its columns (rows). Notice that an irreducible matrix is both row and column allowable. It is easy to verify the validity of the following propositions:

a) **A** is column-allowable if and only if for all non-negative $\mathbf{x} \neq 0$ is $\mathbf{A}\mathbf{x} \neq 0$.

b) for all $p \geq 0$ and all $n \geq p$ is $\mathbf{A}_n \ldots \mathbf{A}_{p+1}\, \mathbf{A}_p$ column-allowable if and only if for all $n \geq 0$ is $\mathbf{A}_n$ column allowable.

These propositions can be interpreted in the following way. It is a necessary and sufficient condition for the population of (21) to be always different from zero (independently of the initial time p and the non-zero population vector $\mathbf{z}_p$ at time p) that all the matrices $\mathbf{A}_n$ be column-allowable. Therefore, in the following we restrict our attention to sequences of environmental conditions represented by column-allowable matrices.

We are ready to introduce in the next theorem the two main results that characterize the asymptotic behavior of (21). The first is due to Seneta (1981) and deals with the strong ergodicity of (21), while the second, which follows as a corollary of the first, characterizes the asymptotic growth rate of (21).

THEOREM 1. *Let $\mathbf{A}_n$, $n \geq 0$ be a sequence of $N \times N$ non-negative and column-allowable matrices that converge to a primitive matrix* **A** *with dominant eigenvalue λ and associated probability normed eigenvector* **v**. *Then for all $p \geq 0$ and all $\mathbf{z}_p \neq 0$ is $\|\mathbf{z}_n\| \neq 0$ and*

$$a)\quad \lim_{n\to\infty} \frac{\mathbf{z}_n}{\|\mathbf{z}_n\|} = \frac{\mathbf{A}_n \ldots \mathbf{A}_{p+1}\mathbf{A}_p\mathbf{z}_p}{\|\mathbf{A}_n \ldots \mathbf{A}_{p+1}\mathbf{A}_p\mathbf{z}_p\|} = \mathbf{v}$$

$$b)\quad \lim_{n\to\infty} \frac{\|\mathbf{z}_{n+1}\|}{\|\mathbf{z}_n\|} = \lim_{n\to\infty} \|\mathbf{z}_n\|^{\frac{1}{n}} = \lim_{n\to\infty} \frac{\|\mathbf{A}_{n+1}\mathbf{A}_n \ldots \mathbf{A}_{p+1}\mathbf{A}_p\mathbf{z}_p\|}{\|\mathbf{A}_n \ldots \mathbf{A}_{p+1}\mathbf{A}_p\mathbf{z}_p\|} = \lambda$$

Proof. Result a) is due to Seneta (1981, pag 96). To obtain result b) lets consider

$$\lim_{n\to\infty} \frac{\|\mathbf{z}_{n+1}\|}{\|\mathbf{z}_n\|} = \lim_{n\to\infty} \frac{\|\mathbf{A}_{n+1}\mathbf{z}_n\|}{\|\mathbf{z}_n\|} = \lim_{n\to\infty} \left\|\mathbf{A}_{n+1} \frac{\mathbf{z}_n}{\|\mathbf{z}_n\|}\right\| = \left\|\lim_{n\to\infty} \mathbf{A}_{n+1} \lim_{n\to\infty} \frac{\mathbf{z}_n}{\|\mathbf{z}_n\|}\right\|$$

since the norm is a continuous mapping. Now, using $\lim_{n\to\infty} \mathbf{A}_{n+1} = \mathbf{A}$ and $\lim_{n\to\infty} \frac{\mathbf{z}_n}{\|\mathbf{z}_n\|} = \mathbf{v}$ we have

$$\lim_{n\to\infty} \frac{\|\mathbf{z}_{n+1}\|}{\|\mathbf{z}_n\|} = \|\mathbf{A}\mathbf{v}\| = \lambda\|\mathbf{v}\| = \lambda$$

for $\mathbf{v}$ is a probability normed vector. $\lim_{n\to\infty}\|\mathbf{z}_n\|^{\frac{1}{n}} = \lambda$ follows from the classical result by which if h_n is a sequence of positive numbers and $\lim_{n\to\infty} \frac{h_{n+1}}{h_n}$ exists then $\lim_{n\to\infty} h_n^{\frac{1}{n}} = \lim_{n\to\infty} \frac{h_{n+1}}{h_n}$.

Asymptotic Relationships for the Macro and Micro Models

In the remaining of this section we will study the property of strong ergodicity and the asymptotic growth rate for the systems (4), (8) and (9) defined in the preceding sections.

Our general assumptions for this section are:

H3. the sequence of matrices $\mathbf{M}_n$ that characterizes the slow dynamics converges to a certain matrix $\mathbf{M}$.

H4. for each $i = 1,\dots,q$, the sequence of matrices $\mathbf{P}_i(n)$ corresponding to the fast dynamics of group i converges to a primitive matrix $\mathbf{P}_i(\infty)$.

Due to the continuity of the eigenvalues as a function of the entries of the matrix, the spectral radius of $\mathbf{P}_i(\infty)$ is 1 for each i. Moreover, taking limits in (3) when $n \to\infty$ we have $\mathbf{e}_i^T\mathbf{P}_i(\infty) = \mathbf{e}_i^T$, i.e., the limit matrix $\mathbf{P}_i(\infty)$ is also stochastic.

Since $\mathbf{P}_i(\infty)$ is primitive we have then

$$\lim_{k\to\infty} \mathbf{P}_i^k(\infty) = \overline{\mathbf{P}}_i(\infty) = \mathbf{v}_i\mathbf{e}_i^T$$

where $\mathbf{v}_i$ is the right eigenvector of $\mathbf{P}_i(\infty)$ associated to eigenvalue 1 and normalized so that $\|\mathbf{v}_i\| = 1$. Therefore, if we define $\mathbf{P} = diag(\mathbf{P}_1(\infty),\mathbf{P}_2(\infty),\dots,\mathbf{P}_q(\infty))$,
$\overline{\mathbf{P}} = diag(\overline{\mathbf{P}}_1(\infty), \overline{\mathbf{P}}_2(\infty),\dots, \overline{\mathbf{P}}_q(\infty))$, and $\mathbf{V} = \mathrm{diag}(\mathbf{v}_1, \mathbf{v}_2,\dots, \mathbf{v}_q)$ we trivially have

$$\lim_{n\to\infty} \mathbf{P}_n = \mathbf{P} \tag{23}$$

$$\lim_{k\to\infty} \mathbf{P}^k = \overline{\mathbf{P}} \tag{24}$$

$$\overline{\mathbf{P}} = \mathbf{V}\mathbf{U} \tag{25}$$

$$\mathbf{U}\mathbf{V} = \mathbf{I}_q \tag{26}$$

As a consequence of both H4 and the continuity of the eigenvalues and eigenvectors of $\mathbf{P}_i(n)$ we have the following Lemma.

LEMMA 2.

a) Sequence $\mathbf{V}_n$ *converges and* $\lim_{n\to\infty} \mathbf{V}_n = \mathbf{V}$

b) Sequence $\overline{\mathbf{P}}_n$ *converges and* $\lim_{n\to\infty} \overline{\mathbf{P}}_n = \overline{\mathbf{P}}$

Proof. a) From theorem 1 (Appendix I) we have that the normalized eigenvectors associated to a simple eigenvalue are continuous functions of the entries of the matrix, and therefore, for each $i = 1,2,\ldots,q$ $\lim_{n\to\infty} \mathbf{P}_i(n) = \mathbf{P}_i(\infty)$ implies $\lim_{n\to\infty} \mathbf{v}_i(n) = \mathbf{v}_i$ and therefore is $\lim_{n\to\infty} \mathbf{V}_n = \mathbf{V}$. b) $\lim_{n\to\infty} \overline{\mathbf{P}}_n = \lim_{n\to\infty} \mathbf{V}_n\mathbf{U} = \mathbf{VU} = \overline{\mathbf{P}}$.

The above results guarantee that the sequence of matrices that represents the aggregated system $\overline{\mathbf{M}}_n = \mathbf{UM}_n\mathbf{V}_n$ converges to matrix $\overline{\mathbf{M}} = \mathbf{UMV}$, which obviously can be interpreted as the matrix that describes the aggregated system for the stabilized environment.

We now introduce two hypothesis that will guarantee that the aggregated system meets the conditions of theorem 1 and is therefore strongly ergodic.

H5. Matrix $\overline{\mathbf{M}}$ is primitive. Let λ be the (algebraically simple) dominant eigenvalue of $\overline{\mathbf{M}}$ and let $\mathbf{r}$ be the probability normed right eigenvector associated to λ.

H6. For all n, $\overline{\mathbf{M}}_n$ is column-allowable. Using lemma 2 we have that this condition is equivalent to the following one: for each n and for each group j, there exists i such that $\mathbf{M}_{ij}(n) \neq 0$, that is, the slow dynamics allows, at every instant, the transition from any group j to at least another group (possibly also group j). Recall that H6 assures population never becomes zero if it is not initially zero.

In this conditions we have as a direct application of theorem 1:

PROPOSITION 3. *Let the aggregated system (9) verify hypothesis H3 to H6. Then, for each* $p \geq 0$ *and for each non-zero condition* $\mathbf{Y}_p$ *at time* p, *we have for the aggregated system:*

$$\lim_{n\to\infty} \frac{\mathbf{Y}_n}{\|\mathbf{Y}_n\|} = \mathbf{r}$$

$$\lim_{n\to\infty} \frac{\|\mathbf{Y}_{n+1}\|}{\|\mathbf{Y}_n\|} = \lim_{n\to\infty} \|\mathbf{Y}_n\|^{\frac{1}{n}} = \lambda$$

In order to relate the spectral properties of matrices $\overline{\mathbf{M}}$ and $\mathbf{M}\overline{\mathbf{P}}$ (which represents the auxiliary system for the stabilized environment), we make use of the following proposition.

PROPOSITION 4. *Matrices* $\mathbf{M}\overline{\mathbf{P}}$ *and* $\mathbf{M}$ *verify:*

a) $\det(\lambda\mathbf{I}_N - \mathbf{M}\overline{\mathbf{P}}) = \lambda^{N-q} \det(\lambda\mathbf{I}_q - \overline{\mathbf{M}})$; *in particular, the dominant eigenvalues of both matrices, together with their respective multiplicities, coincide.*

b) If $\mathbf{r}$ *and* $\mathbf{l}$ *are respectively right and left eigenvectors of* $\overline{\mathbf{M}}$ *associated to* $\lambda \neq 0$ *then* $\mathbf{MVr}$ *and* $\mathbf{U}^T\mathbf{l}$ *are respectively right and left eigenvectors of* $\mathbf{M}\overline{\mathbf{P}}$ *associated to* λ.

Proof. The proof is absolutely analogous to that of proposition 1 just replacing $\overline{\mathbf{P}}_0$ by $\overline{\mathbf{P}}$, $\mathbf{B}$ by $\mathbf{M}$, $\mathbf{C}'$ by $\mathbf{M}\overline{\mathbf{P}}$ and $\overline{\mathbf{C}}$ by $\overline{\mathbf{M}}$.

We shall now give a necessary and sufficient condition for matrix $\mathbf{M\overline{P}}$ to be primitive in terms of the characteristics of the asymptotic slow dynamics.

PROPOSITION 5. *Suppose H3 to H6 hold. Then:*

$\mathbf{M\overline{P}}$ *is primitive if and only if* $\mathbf{M}$ *is row-allowable*

Proof. We know $\overline{\mathbf{M}}$ is primitive; let λ be its (simple) dominant eigenvalue and let $\mathbf{r}$ and $\mathbf{l}$ be its positive right and left eigenvectors. We now apply the following theorem (Berman *et al.*, 1979, pag 42); A non-negative square matrix $\mathbf{A}$ is irreducible if and only if the spectral radius of $\mathbf{A}$ is simple and is associated to positive right and left eigenvectors. According to proposition 4, λ is the spectral radius of $\mathbf{M\overline{P}}$ and besides it is simple, strictly dominant and has associated right and left eigenvectors given by $\mathbf{MVr}$ and $\mathbf{U}^T\mathbf{l}$. Notice that given a positive vector $\mathbf{z}$, $\mathbf{Az}$ is positive if and only if $\mathbf{A}$ is row-allowable. Therefore, since $\mathbf{V}$ and $\mathbf{U}^T$ are row-allowable and $\mathbf{r}$ and $\mathbf{l}$ are positive, $\mathbf{M\overline{P}}$ is irreducible (and consequently primitive, for λ is strictly dominant) if and only if $\mathbf{M}$ is row allowable.

Therefore, we make an additional hypothesis that will guarantee that matrix $\mathbf{M\overline{P}}$ is primitive.

H7. Matrix $\mathbf{M}$ is row-allowable. This can be interpreted by saying that, asymptotically, the slow dynamics verifies that, for $i = 1,2,...,q$ and $j = 1,2,...,N_i$, there exists at least one allowed transition towards subgroup j of group i.

Then the asymptotic behavior of the auxiliary system is given by the following proposition.

PROPOSITION 6. *Lets suppose hypothesis H3 to H7 hold. Then* $\mathbf{M}_n\overline{\mathbf{P}}_n$ *is column-allowable for all* n. *Moreover, for each* $p \geq 0$ *and for each non-zero condition* $\mathbf{X}_p$ *at time* p, *we have for the auxiliary system (8):*

$$\lim_{n\to\infty}\frac{\mathbf{X}_n}{\|\mathbf{X}_n\|}=\frac{\mathbf{MVr}}{\|\mathbf{MVr}\|}$$

$$\lim_{n\to\infty}\frac{\|\mathbf{X}_{n+1}\|}{\|\mathbf{X}_n\|}=\lim_{n\to\infty}\|\mathbf{X}_n\|^{\frac{1}{n}}=\lambda$$

Proof. Matrix $\mathbf{M}_n\overline{\mathbf{P}}_n$ has the form

$$\mathbf{M}_n\overline{\mathbf{P}}_n=\begin{pmatrix}\mathbf{M}_{11}\overline{\mathbf{P}}_1(n) & \mathbf{M}_{12}\overline{\mathbf{P}}_2(n) & \cdots & \mathbf{M}_{1q}\overline{\mathbf{P}}_q(n)\\ \mathbf{M}_{21}\overline{\mathbf{P}}_1(n) & \mathbf{M}_{22}\overline{\mathbf{P}}_2(n) & \cdots & \mathbf{M}_{2q}\overline{\mathbf{P}}_q(n)\\ \vdots & \vdots & \ddots & \vdots\\ \mathbf{M}_{q1}\overline{\mathbf{P}}_1(n) & \mathbf{M}_{q2}\overline{\mathbf{P}}_2(n) & \cdots & \mathbf{M}_{qq}\overline{\mathbf{P}}_q(n)\end{pmatrix}$$

H6 together with lemma 2 implies that, for each $j = 1,...,q$ and each n, there exists $i = i(j,n)$ such that $\mathbf{M}_{ij}(n) \neq 0$ and, since the $\overline{\mathbf{P}}_i(n)$ are positive matrices, then $\mathbf{M}_{ij}(n)\overline{\mathbf{P}}_j(n)$ has at least a positive row, and consequently $\mathbf{M}_n\overline{\mathbf{P}}_n$ is column-allowable. Proposition 4 guarantees that $\mathbf{M\overline{P}}$ is primitive and then the result follows as a direct application of theorem 1.

Let us proceed to the study of the asymptotic behavior of the microsystem (4). This system is represented, for the stabilized environment, by matrix $\mathbf{MP}^k = \lim_{n\to\infty} \mathbf{M}_n\mathbf{P}_n^k$. In the first place we relate the incidence matrices of the original and perturbed systems for all times n as well as asymptotically.

PROPOSITION 7. *There exists a positive integer k_0 such that for all $k \geq k_0$ we have:*

a) for all n is $\mathbf{M}_n\overline{\mathbf{P}}_n \sim \mathbf{M}_n\mathbf{P}_n^k$

b) $\mathbf{M}\overline{\mathbf{P}} \sim \mathbf{MP}^k$

Proof. Let i be fixed. Since $\mathbf{P}_i(n)$ is primitive for all n and so is $\mathbf{P}_i(\infty)$, we know (Horn & Johnson, 1985, pag 520) that for all $k \geq N_i^2 - 2N_i + 2$ is $\mathbf{P}_i^k(n) > 0$ and $\mathbf{P}_i^k(\infty) > 0$. Taking into account that $\overline{\mathbf{P}}_i(\infty)$ and $\overline{\mathbf{P}}_i(n)$ are positive matrices, if we choose $k_0 = N_{\max}^2 - 2N_{\max} + 2$, where $N_{\max} = \max\{N_1, \ldots, N_q\}$ we have that for all $k \geq k_0$, all i and all n is $\overline{\mathbf{P}}_i(n) \sim \mathbf{P}_i^k(n)$ and $\overline{\mathbf{P}}_i(\infty) \sim \mathbf{P}_i^k(\infty)$. Therefore, for all $k \geq k_0$ is $\overline{\mathbf{P}} \sim \mathbf{P}^k$ and $\overline{\mathbf{P}}_n \sim \mathbf{P}_n^k$ for all n, so is $\mathbf{M}\overline{\mathbf{P}} \sim \mathbf{MP}^k$ and $\mathbf{M}_n\overline{\mathbf{P}}_n \sim \mathbf{M}_n\mathbf{P}_n^k$ as we wanted to show.

Notice that this proposition, together with hypothesis H3 to H6, guarantees that for sufficiently large k, $\mathbf{M}_n\mathbf{P}_n^k$ is column-allowable and $\mathbf{MP}^k$ is primitive (recall that the primitivity or non-primitivity of a non-negative matrix only depends on its incidence matrix and not on the actual values of its non-zero entries).

We now consider matrix $\mathbf{MP}^k$ as a perturbation of $\mathbf{M}\overline{\mathbf{P}}$ in the following way

$$\mathbf{MP}^k = \mathbf{M}\overline{\mathbf{P}} + \mathbf{M}(\mathbf{P}^k - \overline{\mathbf{P}})$$

and make use of perturbation theory.

Let us consider the eigenvalues of $\mathbf{P}$ ordered by decreasing modulus (notice that the eigenvalues of $\mathbf{P}$ are the union of those of the different $\mathbf{P}_i(\infty)$)

$$1 = \lambda_1 = \cdots = \lambda_q > |\lambda_{q+1}| \geq \cdots \geq |\lambda_N|$$

and let

$$\beta > |\lambda_{q+1}| \tag{27}$$

i.e., β is any real number greater than the modulus of the greater "subdominant" eigenvalue of the $\mathbf{P}_i(\infty)$ (notice that β can always be taken smaller than 1). Then we have

PROPOSITION 8. *If* $\|*\|$ *is any consistent matrix norm in the space of real matrices* $N \times N$ *then*

$$\left\|\mathbf{M}(\mathbf{P}^k - \overline{\mathbf{P}})\right\| = o(\beta^k) \quad when \quad k \to \infty$$

Proof. The proof is absolutely analogous to the first part of proposition 3 where we showed $\mathbf{M}_n(\mathbf{P}_n^k - \overline{\mathbf{P}}_n) = o(\alpha^k)$, $k \to \infty$, replacing $\mathbf{M}_n$ by $\mathbf{M}$, $\mathbf{P}_n$ by $\mathbf{P}$ and $\overline{\mathbf{P}}_n$ by $\overline{\mathbf{P}}$.

We are now ready to characterize the asymptotic behavior of system (4) in terms of that of the aggregated system (9).

PROPOSITION 9. *If hypothesis H3 to H7 hold there exists k_0 such that for each $k \geq k_0$ we have: a) for all n is $\mathbf{M}_n\mathbf{P}_n^k$ column-allowable. b) for each $p \geq 0$ and for each non-zero condition $\mathbf{X}_p$ at time p, the microsystem (4) verifies*

$$\lim_{n\to\infty}\frac{\mathbf{X}_n}{\|\mathbf{X}_n\|}=\frac{\mathbf{MVr}}{\|\mathbf{MVr}\|}+o(\beta^k),\quad k\to\infty$$

$$\lim_{n\to\infty}\frac{\|\mathbf{X}_{n+1}\|}{\|\mathbf{X}_n\|}=\lim_{n\to\infty}\|\mathbf{X}_n\|^{\frac{1}{n}}=\lambda+o(\beta^k),\quad k\to\infty$$

where β is any number verifying (27).

Proof. a) From proposition 6 is $\mathbf{M}_n\overline{\mathbf{P}}_n$ column-allowable and therefore, using proposition 7, we have that for all n and all k greater than a certain k_1 is $\mathbf{M}_n\mathbf{P}_n^k$ column-allowable too.

b) We know from proposition 6 that $\mathbf{M}\overline{\mathbf{P}}$ is primitive. Therefore proposition 7 guarantees that for $k \geq k_1$ is $\mathbf{MP}^k$ also primitive. We have as well (proposition 8) that λ and $\mathbf{MVr}$ are the spectral radius of $\mathbf{M}\overline{\mathbf{P}}$ and an associated right eigenvector respectively. A reasoning similar to that of proposition 4 (based in the perturbation theorem 1) yields that for all k greater than a certain k_2, matrix $\mathbf{MP}^k$ has a simple and strictly dominant eigenvalue $\lambda + o(\beta^k)$ associated to which we have the right eigenvector $\mathbf{MVr} + o(\beta^k)$. Therefore, setting $k_0 = \max\{k_1, k_2\}$ we have that for all $k \geq k_0$ theorem 1 guarantees

$$\lim_{n\to\infty}\frac{\mathbf{X}_n}{\|\mathbf{X}_n\|}=\frac{\mathbf{MVr}+o(\beta^k)}{\|\mathbf{MVr}+o(\beta^k)\|}=\frac{\mathbf{MVr}}{\|\mathbf{MVr}\|}+o(\beta^k),\quad k\to\infty$$

$$\lim_{n\to\infty}\frac{\|\mathbf{X}_{n+1}\|}{\|\mathbf{X}_n\|}=\lim_{n\to\infty}\|\mathbf{X}_n\|^{\frac{1}{n}}=\lambda+o(\beta^k),\quad k\to\infty$$

as we wanted to prove.

Stabilizing Demography and Migration

We shall now illustrate the results of this section showing how they could be applied to the case of the model proposed in section 2.3 under the hypothesis of time variable demography and migration tending to an equilibrium. We have then that all the fertility and survival coefficients approach a limit, i.e., $F_{kl}^i(n) \underset{n\to\infty}{\to} F_{kl}^i$, $k = 1,\dots,N^i$; $l = 1,\dots,N^i$; $i = 1,\dots,q$ and $S_{kl}^i(n) \underset{n\to\infty}{\to} S_{kl}^i$, $k = 1,\dots, N^{i+1}$; $l = 1,\dots,N^i$; $i = 1,\dots, q-1$. Besides, for all $i = 1,\dots,q$ the migration matrices $\mathbf{P}_i(n)$ converge to some primitive matrix $\mathbf{P}_i(\infty)$ (so that H3 and H4 hold).

It is easy to check that sufficient conditions for H5 to H7 to be verified are:

a) For all times, and also in the limit, the internal survival coefficients for all patches and for all ages are non-zero, i.e., $S_{ll}^i(n) \neq 0$ and $S_{ll}^{ii} \neq 0$ for all n, i and l.

b) For all times, and also in the limit, the internal fertility coefficients for all patches for the last age group are non-zero, i.e., $S_{il}^{q}(n) \neq 0$ and $S_{il}^{q} \neq 0$ for all n, i and l.

c) Asymptotically there exists at least a non-zero fertility coefficient for an age i (i.e., $\mathbf{F}_i \neq 0$) such that $m.c.d(i,q) = 1$.

The above assumptions guarantee that all the results developed in this section are valid for our slow demography-fast migration model. Then, independently of the initial time $p \geq 0$ where we consider our biological system starting to evolve and independently of the non-zero initial population vector $\mathbf{X}_p$, the aggregated system will asymptotically have a fixed growth rate and a fixed population structure. Let us suppose that the asymptotic growth rate for the aggregated system is λ while the asymptotic population structure is given by vector $\mathbf{r}$. Then, the original system will also have an asymptotically stable growth rate and a population structure, that are given by $\lambda + o(\beta^k)$ and $\mathbf{r} + o(\beta^k)$ respectively. As in the case of a cyclically varying environment, the greater the ratio between the characteristic times of demography and migration is, the more accurate the approximation of the asymptotic features of the microsystem will be.

5. CONCLUSION

The method here developed allows one to aggregate a time varying complex system with two time scales to obtain a reduced time varying aggregated system that shows, in the cases of cyclical and stabilizing temporal variation explored, similar asymptotic features to those of the general system. Besides, the parameters of the aggregated system can be easily expressed as functions of the slow dynamics and of the equilibrium proportions of individuals corresponding to the fast dynamics. In this way, it is possible to study how changes in the fast dynamics affect the dynamics of the aggregated system.

In future contributions we plan to extend the study of aggregation in time varying environments to more general kinds of temporal variation. In particular, it would be appealing to study whether the weak ergodicity of the aggregated system (tendency of the system to forget its past, see Cohen (1979a)) translates to the general system.

In our model we have supposed the fast dynamics to be a conservative process (migration, activity changes, etc.). It would be interesting to explore whether this can be generalized to account for more general fast dynamics. For example, in the context of population genetic models the gene changes are usually slow in comparison to the demography of a population (Charlesworth, 1980). So we might be interested in knowing how the age structure of a population affects the genetic material of the individuals, considering models in which the fast dynamics correspond to the demographic process.

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APPENDIX

Proof of proposition 1. a) It is trivial to show that $\overline{\mathbf{P}}_0$ is a projector over the subspace in R^N spanned by the columns of $\mathbf{V}_0$, so Im $\overline{\mathbf{P}}_0 \oplus$ ker $\overline{\mathbf{P}}_0 = R^N$ and dim(Im $\overline{\mathbf{P}}_0$) = q, dim(ker $\overline{\mathbf{P}}_0$) = $N - q$. Therefore, if $\mathbf{K}$ is a matrix whose columns constitute an arbitrary base of ker $\overline{\mathbf{P}}_0$ then the columns of $(\mathbf{V}_0 \mid \mathbf{K})$ are a basis of R^N. The expression $\mathbf{X}$ of operator $\mathbf{C}' = \mathbf{B}\overline{\mathbf{P}}_0$ respect to this base will therefore be $\mathbf{X} = (\mathbf{V}_0 \mid \mathbf{K})^{-1} = \mathbf{B}\overline{\mathbf{P}}_0\,(\mathbf{V}_0 \mid \mathbf{K})$. Since $\mathbf{U}\mathbf{V}_0 = \mathbf{I}_q$ and $\mathbf{U}K = \mathbf{U}\overline{\mathbf{P}}_0\mathbf{K} = 0$ we have that $(\mathbf{V}_0 \mid \mathbf{K})^{-1} = \left(\frac{\mathbf{U}}{\mathbf{U}'}\right)$ where $\mathbf{U}'$ is an appropriate matrix. Therefore

$$\mathbf{X} = \left(\frac{\mathbf{U}}{\mathbf{U}'}\right)\mathbf{B}\overline{\mathbf{P}}_0(\mathbf{V}_0 \mid \mathbf{K}) = \left(\frac{\mathbf{U}}{\mathbf{U}'}\right)(\mathbf{B}\overline{\mathbf{P}}_0\mathbf{V}_0 \mid 0) = \begin{pmatrix} \overline{\mathbf{C}} & 0 \\ \mathbf{U}'\mathbf{B}\overline{\mathbf{P}}_0 & 0 \end{pmatrix}$$

where we have used $\overline{\mathbf{C}} = \mathbf{U}\mathbf{C}'\mathbf{V}_0$. Since $\mathbf{C}'$ and $\mathbf{X}$ are similar they have the same characteristic polynomial and we have $\det(\lambda\mathbf{I}_N - \mathbf{C}') = \lambda^{N-q}\det(\lambda\mathbf{I}_q - \overline{\mathbf{C}})$ as we wanted to prove.

b) We know $\overline{\mathbf{C}}\mathbf{r} = \lambda\mathbf{r} \neq 0$, i.e. $\mathbf{U}\mathbf{B}\mathbf{V}_0\mathbf{r} = \lambda\mathbf{r} \neq 0$ so it must be $\mathbf{B}\mathbf{V}_0\mathbf{r} \neq 0$. Besides

$$\mathbf{C}'\mathbf{B}\mathbf{V}_0\mathbf{r} = \mathbf{B}\overline{\mathbf{P}}_0\mathbf{B}\mathbf{V}_0\mathbf{r} = \mathbf{B}\mathbf{V}_0\mathbf{U}\mathbf{B}\mathbf{V}_0\mathbf{r} = \mathbf{B}\mathbf{V}_0\overline{\mathbf{C}}\mathbf{r} = \lambda\mathbf{B}\mathbf{V}_0\mathbf{r}$$

so $\mathbf{B}\mathbf{V}_0\mathbf{r}$ is right eigenvector of $\mathbf{C}'$ associated to λ.

We also know $\mathbf{l}^T\overline{\mathbf{C}} = \lambda\,\mathbf{l}^T \neq 0$, i.e., $\mathbf{l}^T\mathbf{U}\mathbf{B}\mathbf{V}_0 = \lambda\mathbf{l}^T \neq 0$, so it must be $\mathbf{l}^T\mathbf{U} \neq 0$. Then, multiplying on the right by $\mathbf{U}$ we have $\mathbf{l}^T\mathbf{U}\mathbf{B}\mathbf{V}_0\mathbf{U} = \lambda\mathbf{l}^T\mathbf{U}$, i.e., $\mathbf{l}^T\mathbf{U}\mathbf{B}\overline{\mathbf{P}}_0 = \mathbf{l}^T\mathbf{U}\mathbf{C}' = \lambda\mathbf{l}^T\mathbf{U}$ as we wanted to prove.

Proof of proposition 3. We first show that for all $n = 0,1,\ldots$ is $\mathbf{M}_n\left(\mathbf{P}_n^k - \overline{\mathbf{P}}_n\right) = o(\alpha^k)$, $k \to \infty$. Let us fix n and consider a Jordan canonical decomposition of $\mathbf{P}_n$. Eigenvalue 1 is simple and strictly dominant for each of the $\mathbf{P}_i(n)$ and is associated to right and left eigenvectors $\mathbf{v}_i(n)$ and $\mathbf{e}_i$. Therefore, we have that for matrix $\mathbf{P}_n$ eigenvalue 1 is strictly dominant, semi-simple and has multiplicity q . Besides the columns of $\mathbf{V}_n$ and the rows of $\mathbf{U}$ are bases of its associated right and left eigenspaces respectively. Since $\mathbf{U}\mathbf{V}_n = \mathbf{I}_q$ we have that a Jordan decomposition of $\mathbf{P}_n$ with eigenvalues ordered by decreasing modulus will have the form:

$$\mathbf{P}_n = \left(\mathbf{V}_n \mid \mathbf{V}_n'\right) diag(\mathbf{I}_q, \mathbf{H})\left(\frac{\mathbf{U}}{\mathbf{U}'}\right)$$

where $\mathbf{V}_n'$ and $\mathbf{U}'$ are appropriate matrices and $\mathbf{H}$ corresponds to Jordan blocks associated to eigenvalues $\lambda_{q+1}(n), \ldots, \lambda_N(n)$ (of modulus strictly less than α) . Therefore taking into account that $\overline{\mathbf{P}}_n = \mathbf{V}_n\mathbf{U}$ is

$$\mathbf{P}_n^k = \overline{\mathbf{P}}_n + \left(\mathbf{V}_n \mid \mathbf{V}_n'\right) diag(0, \mathbf{H}^k)\left(\frac{\mathbf{U}}{\mathbf{U}'}\right)$$

so

$$\frac{\mathbf{M}_n(\mathbf{P}_n^k - \overline{\mathbf{P}}_n)}{\alpha^k} = \mathbf{M}_n\left(\mathbf{V}_n \mid \mathbf{V}_n'\right) diag\left(0, \left(\frac{\mathbf{H}}{\alpha}\right)^k\right)\left(\frac{\mathbf{U}}{\mathbf{U}'}\right)$$

and taking limits $k \to \infty$ we have $\mathbf{M}_n\left(\mathbf{P}_n^k - \overline{\mathbf{P}}_n\right) = o(\alpha^k)$, $k \to \infty$. Therefore we have

$$\begin{aligned} \mathbf{C}(k) &= \mathbf{M}_{T-1}\mathbf{P}_{T-1}^k \ldots \mathbf{M}_1\mathbf{P}_1^k \mathbf{M}_0\mathbf{P}_0^k = \\ &= \left(\mathbf{M}_{T-1}\overline{\mathbf{P}}_{T-1} + o(\alpha^k)\right)\ldots\left(\mathbf{M}_1\overline{\mathbf{P}}_1 + o(\alpha^k)\right)\left(\mathbf{M}_0\overline{\mathbf{P}}_0 + o(\alpha^k)\right) = \\ &= \mathbf{M}_{\tau-1}\overline{\mathbf{P}}_{\tau-1}\ldots\mathbf{M}_1\overline{\mathbf{P}}_1\mathbf{M}_0\overline{\mathbf{P}}_0 + o(\alpha^k) = \mathbf{C}' + o(\alpha^k) \end{aligned}$$

as we wanted to prove.

Below we state the main result about matrix perturbation that is used in this work (see Stewart, 1990).

THEOREM 1. *Let λ be a simple eigenvalue of a matrix* $\mathbf{A}$ *of dimensions* $N \times N$ *with associated right and left eigenvectors,* $\mathbf{x}_r$ *and* $\mathbf{x}_l$ *, respectively. Let* $\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{E}$ *be a perturbation of matrix* $\mathbf{A}$, and $\|*\|$ *any consistent matrix norm in the space of matrices* $N \times N$. *Then*

a) there exists a unique eigenvalue $\tilde{\lambda}$ of $\tilde{\mathbf{A}}$ such that :

$$\tilde{\lambda} = \lambda + \frac{\mathbf{x}_l^T \mathbf{E} \mathbf{x}_r}{\mathbf{x}_l^T \mathbf{x}_r} + O\left(\|\mathbf{E}\|^2\right)$$

b) associated to $\tilde{\lambda}$ there exist right and left eigenvectors $\tilde{\mathbf{x}}_r$ and $\tilde{\mathbf{x}}_l$ respectively such that:

$$\tilde{\mathbf{x}}_r = \mathbf{x}_r + O(\|\mathbf{E}\|)$$
$$\tilde{\mathbf{x}}_l = \mathbf{x}_l + O(\|\mathbf{E}\|)$$

c) for small enough $\|\mathbf{E}\|$, $\tilde{\lambda}$ is the only eigenvalue of $\tilde{\mathbf{A}}$ in a certain neighbourhood of λ (therefore, if λ is strictly dominant for $\mathbf{A}$, so will be $\tilde{\lambda}$ for $\tilde{\mathbf{A}}$).

Proof of proposition 4. We know $\mathbf{C}(k) = \mathbf{C}' + \mathbf{E}$ with $\mathbf{E} = \mathbf{C}(k) - \mathbf{C}' = o(\alpha^k)$ by proposition 3. Therefore using theorem 1 we have that for sufficiently large k , $\mathbf{C}(k)$ has a strictly dominant and simple eigenvalue μ_k in the form

$$\mu_k = \mu + \frac{\left\langle \mathbf{U}^T \mathbf{l}, \left(\mathbf{C}(k) - \mathbf{C}'\right)\mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle}{\left\langle \mathbf{U}^T \mathbf{l}, \mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle} + O(o(\alpha^k)^2)$$

associated to which there are right and left eigenvectors in the form $\mathbf{BV}_0\mathbf{r} + O(o(\alpha^k))$ and $\mathbf{U}^T\mathbf{l} + O(o(\alpha^k))$ respectively. Since $O(o(\alpha^k)) = o(\alpha^k)$ all we have to do for the proposition to hold is to show that $\frac{\left\langle \mathbf{U}^T \mathbf{l}, \left(\mathbf{C}(k) - \mathbf{C}'\right)\mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle}{\left\langle \mathbf{U}^T \mathbf{l}, \mathbf{M}_0\mathbf{V}_0\mathbf{r}\right\rangle} = o(\alpha^k)$ which is immediate since $\mathbf{C}(k) - \mathbf{C}' = o(\alpha^k)$ and the scalar product is a continuous function.